

# A nonlocal spatial model for savannas

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## Abstract

We propose a model equation for the dynamics of tree density in savannas. It only considers long-range competition among trees and the effect of fire, and despite short-range facilitation is not taken into account, we recover the standard spatial patterns observed in realistic situations. Therefore we show that facilitation is not a key ingredient in the modelling of savannas. We also study how fires affect the survival of trees in the long time limit as well as the maintenance of the patterns.

**Keywords:** pattern formation, nonlinear dynamics, stochastic processes.

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## 1. Introduction

Savannas ecosystems are characterized by the long-term coexistence between a continuous grass layer and scattered or clustered trees [1]. Occurring in many regions of the world, in areas with very different climatic and ecological conditions, the spatial structure, persistence, and resilience of savannas have long intrigued ecologists [2–4]. However, despite substantial research, the origin and nature of savannas have not yet been well explained.

Savanna tree populations often exhibit pronounced, non-random spatial structure [5–10]. Much research has therefore focused on explaining how spatial patterning in savannas arises [7–9, 11, 12]. It has frequently been claimed that spatial pattern in savanna vegetation can be explained by a combination of long-distance inhibition and short-distance facilitation [13–16]. This combination of mechanisms is known to produce patterns in many other natural systems. While the facilitation component has often been thought to be a key component in previous savanna studies [9, 15, 17, 18], Rietkerk and Van de Koppel [8], based on a review of spatial patterns observed in diverse ecosystems, suggested that only the long-distance competition part is key to pattern formation. To our knowledge, this explanation has not been explored for a savanna system. On the other hand, a similar mechanism

of competitive interactions between species, similar to the one presented here for savannas, has been shown to give rise to clusters of species in the context of classical ecological niche theory. Scheffer and van Nes [19] showed that species distribution in niche space was clustered, and Pigolotti et al. [20] showed that this arises as an instability of the nonlocal nonlinear equation describing the competition of species.

In the study of savannas, exploring whether or not long-range competition, acting nonlinearly alone or in combination with some others mechanisms, can account for spatial patterning is important because the issue of short-range facilitation among savanna trees has been highly contentious. Some authors have presented evidence of short-distance facilitation [6, 9], while others have demonstrated evidence of short-range competition [5, 7, 10], with conflicting reports sometimes arriving from the same regions. Indeed, the most frequently invoked mechanism of short-range facilitation in savannas, that tree clumps promote infiltration of rainwater that would instead become runoff on patches of bare or sparsely-vegetated ground [15, 21], seems unlikely to apply to all savannas that display spatial pattern. The local infiltration mechanism seems most plausible for extremely arid systems, where there is substantial bare ground that acts as a barrier to infiltration. For mesic to wet savannas, the infiltration mechanism may not be as important because much more of the ground is covered by vegetation. Under these conditions, however, substantial competition among trees may still occur for water or other limiting resources. The root architecture of savanna trees and shrubs, with lateral roots of many

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species extending several meters in each direction, provides a clear physical mechanism by which non-local competition for water or other resources could be mediated [4, 22].

Here we develop a minimalistic model of savannas that considers two of the factors that are thought to be crucial to structure semi-arid to mesic savannas: tree-tree competition and fire. Our main focus is on spatially nonlocal competition, and employing standard tools used in the study of pattern formation phenomena in physics (stability analysis and the structure function), we explore the conditions under which it can produce non-homogeneous spatial distributions. We also include the effect of fires as a function of the local density of trees. We will show how important fires are in the survival of vegetation, i.e., in the long-term coexistence of trees and grass. On the other hand, fire does not play a crucial role in the emergence of spatial structures in our model: we observe the same sequence of patterns when competition intensity is manipulated, independently of the frequency of fires. Competition is therefore the main mechanism governing the formation of spatial structures. We further examine the role of demographic stochasticity in modifying both spatial patterns and the conditions under which trees persist in the system in the presence of fire. Our model is inspired by the one presented by Calabrese et al. in [11], and complements their work, providing further analytical results.

Our results clearly demonstrate that this simple system, with no short-range facilitation, can produce the full spectrum of spatial patterns reported from models employing both short-range facilitation and long-range inhibition (competition). We conclude by discussing the implications of these results for the debate on whether the balance of short-range processes affecting savanna trees is positive, negative, or is variable among systems. To complete our work we include an appendix where we study the effect of external fluctuations (mimicking for e.g. rainfall) on savanna dynamics.

## 2. The Deterministic Model

In this section we derive the deterministic evolution equation for the local density of trees, such that dynamics is of logistic type and we only consider tree-tree competition and fire. We study the formation of patterns via stability analysis and provide numerical simulations of our model, showing the emergence of spatial structures.

### 2.1. The nonlocal savanna model

In [11] it is introduced a simple discrete particle model on a lattice for a savanna system that considers the birth-death dynamics of trees, and where tree-tree competition and fire are the principal ingredients. It is derived a deterministic differential equation describing the time evolution of the global density of trees,  $\rho(t)$ , that reads:

$$\frac{d\rho}{dt} = bP_E(\rho)\rho(t)(1 - \rho(t)) - \alpha\rho(t), \quad (1)$$

where  $\alpha$  and  $b$  are the death and birth rates, respectively, and  $P_E(\rho)$  is the probability of establishment given that a seed has been dispersed. Because competition and fire are independent,  $P_E = P_C P_F$ , where  $P_C$  is the probability of surviving the competition, and  $P_F$  is the probability of surviving a fire event.

Generalizing Eq. (1), we propose an evolution equation for the space-dependent (local) density of trees,  $\rho(\mathbf{x}, t)$ :

$$\frac{\partial\rho(\mathbf{x}, t)}{\partial t} = bP_E\rho(\mathbf{x}, t)(1 - \rho(\mathbf{x}, t)) - \alpha\rho(\mathbf{x}, t). \quad (2)$$

We allow the probability of overcoming competition to depend on tree crowding in a local neighborhood, decaying exponentially with the density of surrounding trees as

$$P_C = \exp\left(-\delta \int G(\mathbf{x} - \mathbf{r})\rho(\mathbf{r}, t)d\mathbf{r}\right), \quad (3)$$

where  $\delta$  is a parameter that modulates the strength of the competition, and  $G(\mathbf{x})$  is a positive kernel function that introduces a finite range of influence.  $P_F$  depends on the local density of grass,  $1 - \rho(\mathbf{x}, t)$ , as

$$P_F = \frac{\sigma}{\sigma + 1 - \rho(\mathbf{x}, t)}, \quad (4)$$

where  $\sigma$  governs the resistance to fire. Notice how our model is close to the one in [11] through the definitions of  $P_C$  and  $P_F$ . The deterministic evolution equation that considers tree-tree competition and fire for the spatial tree density is

$$\frac{\partial\rho(\mathbf{x}, t)}{\partial t} = b_{eff}(\rho)\rho(\mathbf{x}, t)(1 - \rho(\mathbf{x}, t)) - \alpha\rho(\mathbf{x}, t), \quad (5)$$

where

$$b_{eff}(\rho) = \frac{b e^{-\delta \int G(\mathbf{x} - \mathbf{r})\rho(\mathbf{r}, t)d\mathbf{r}} \sigma}{\sigma + 1 - \rho(\mathbf{x}, t)}. \quad (6)$$

Thus, we have a logistic-type equation with an effective growth rate that depends nonlocally on the density itself.

One could include a diffusion term like  $D(\rho)\nabla^2\rho$  in Eq. (5) to account for local dispersal of trees (that may

reflect local seed dispersal giving rise to adult trees) [23, 24]. Though we are interested in isolating the effect of competition among trees and fires, its possible consequences are discussed in the section 4.

As noticed before, the idea behind the nonlocal competition is to capture the effect of the long roots of a tree. Thus the *nonlocal* interaction scale is of the order of the length of the roots [2]. Since the roots are the responsible for the adsorption of resources (water and soil nutrients), a strong long-range competition term implies strong resource depletion.

Since we are interested in the effect of competition and fire on the distribution of savanna vegetation, we will try to fix all the parameters but  $\sigma$  and  $\delta$ . Firstly, (as in [11]) the death rate is taken  $\alpha = 1$ , which can be accomplished by properly rescaling time. We can also fix the growth rate  $b$  by considering the homogenous solution of Eq. (5),  $\rho_0 = \rho_0(b, \sigma, \delta)$ . It can be obtained by solving

$$b_{eff}(\rho_0)(1 - \rho_0) - 1 = 0, \quad (7)$$

with real data from African savannas featuring intermediate to high mean annual precipitation levels [3, 25], for which competition for water is no longer limiting ( $\delta = 0$ ) and fire is not an issue ( $\sigma \rightarrow \infty$ ). In this limit, the upper tree cover has been measured around  $\rho_0 = 0.8$ , and the stationary solution of the model depends only on the birth rate

$$\rho_0(\sigma \rightarrow \infty) = \frac{b-1}{b}, \quad (8)$$

which yields  $b = 5$  solving for a fixed  $\rho_0 = 0.8$  ([11]). In the following we just consider the dependence of our results on  $\delta$  and  $\sigma$ . In particular,  $\rho_0 = \rho_0(\sigma, \delta)$ .

One of the characteristics of this model that makes it suitable for modelling savannas is the long-term coexistence between grass and trees, characteristic of these ecosystems and shown by our equation. To explore it, we study the long-time behavior of the system and analyze the stationary solutions of Eq. (5), which has two fixed points. The first one is the absorbing state representing the absence of trees,  $\rho_0 = 0$ , and the other can be obtained, in the general case, solving Eq. (7) numerically. In the regime where  $\rho_0$  is small (near the critical point), if competition intensity,  $\delta$ , is also small, it is possible to obtain an analytical expression for the critical value of the probability of surviving a fire,  $\sigma^*$ , which is independent of the strength of competition

$$\sigma^* = \frac{1}{b-1}, \quad (9)$$

i.e.  $\sigma^* = 0.25$  for  $b = 5$ . Outside of the limit where  $\delta \ll 1$ , we can solve Eq. (7) numerically in  $\rho_0$  to show

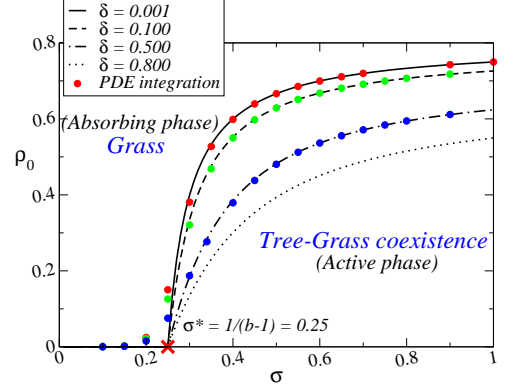


Figure 1: Grass-coexistence phase transition. The lines come from the mean field solution, Eq. (7), and the dots from the numerical integration of the PDE, Eq. (5) in a region of 1 ha. Notice the finite-size effect in the shift of the critical point in the dots. Nevertheless, its value remains independent of  $\delta$ , as expected.

that the critical value of the fire resistance parameter,  $\sigma^*$ , also does not depend on competition.

For higher fire survival probability a steady state with trees is stable (Fig. 1). The model, then, shows a transition from a state where grass is the only form of vegetation to another state where trees and grass coexist at  $\sigma^*$ .

## 2.2. Linear stability analysis

The spatial patterns appearing in the nonlocal savanna model can be studied by performing a linear stability analysis [26] of the stationary homogeneous solutions of equation (5),  $\rho_0 = \rho_0(\sigma, \delta)$ . The stability analysis of  $\rho_0$  is performed by considering small harmonic perturbations around it,  $\rho(\mathbf{x}, t) = \rho_0 + \epsilon e^{i\mathbf{k} \cdot \mathbf{x} - \lambda t}$ ,  $\epsilon \ll 1$ . After some calculations (Appendix A), one arrives at the dispersion relation

$$\lambda(k; \sigma, \delta) = b_{eff}(\rho_0) \frac{1 + \sigma(1 - 2\rho_0)}{\sigma - \rho_0 + 1} - b_{eff}(\rho_0) \frac{\rho_0 [2 - \rho_0 + \delta \hat{G}(k)(\rho_0 - 1)(\rho_0 - 1 - \sigma)]}{(\sigma - \rho_0 + 1)} - 1, \quad (10)$$

where  $\hat{G}(k)$ ,  $k = |\mathbf{k}|$ , is the Fourier transform of the kernel,

$$\hat{G}(\mathbf{k}) = \int G(\mathbf{x}) e^{-i\mathbf{k} \cdot \mathbf{x}} d\mathbf{x}. \quad (11)$$

The critical values of the parameters of the transition to pattern,  $\delta_c$  and  $\sigma_c$ , and the fastest growing wavenumber  $k_c$  are obtained from the simultaneous solution of

$$\lambda(k_c; \sigma_c, \delta_c) = 0, \quad (12)$$

$$\left( \frac{\partial \lambda}{\partial k} \right)_{k_c; \sigma_c, \delta_c} = 0. \quad (13)$$

Note that  $k_c$  represents the most unstable mode of the system, which means it grows faster than the others and eventually dominates the state of the system.

Therefore, it determines the length scale of the spatial pattern. These two equations yield the values of the parameters  $\delta$  and  $\sigma$  at which the maximum of the curve  $\lambda(k)$ , right at  $k_c$ , starts becoming positive. This signals the formation of patterns in the solutions of Eq. (5). As Eq. (13) is explicitly written as

$$\lambda'(k_c) = b_{eff}(\rho_0)\delta\rho_0\hat{G}'(k_c)(\rho_0 - 1), \quad (14)$$

the most unstable wavenumber  $k_c$  can be obtained by evaluating the zeros of the Fourier transform of the kernel.

Equation (10) shows that competition, through the kernel function, fully determines the formation of patterns in the system. If the Fourier transform of  $G$  never takes positive values then  $\lambda(k; \sigma, \delta)$  is always negative and only the homogenous solution is stable. However, when  $\hat{G}$  can take negative solutions then patterns may appear in the system. What does this mean in biological terms? Imagine that we have a family of kernels described by a parameter  $p$ :  $G(\mathbf{x}) = \exp(-|\mathbf{x}|/R)^p$  ( $R$  gives the range of competition). The kernels are more peaked around  $\mathbf{x} = 0$  for  $p < 2$  and more box-like when  $p > 2$ . It turns out that this family of functions has non-negative Fourier transform for  $0 \leq p < 2$ , so that no patterns appear in this case. A lengthy discussion of this property in the context of competition of species can be found in [20]. Thus, the shape of the competition kernel dictates whether or not patterns will appear in the system. If pattern formation is possible, then the values of the fire and competition parameters govern the type of solution (see below).

Our central result for nonlocal competition is that, contrary to conventional wisdom, it can, by itself *promote* the clustering of trees. Whether or not this occurs depends entirely on the shape of the competition kernel. For large  $p$  we have a box-like shape, and in these cases trees compete strongly with other trees, roughly within a distance  $R$  from their position. The mechanism behind this counterintuitive result is that trees farther than  $R$  away from a resident tree area are not able to *invade* it (their seeds do not establish there), so that an exclusion zone develops around it. For smaller  $p$  there is less competition and the exclusion zones disappear.

For a more detailed analysis, one must choose an explicit form for the kernel function. Our choice is determined by the original  $P_C$  taken in [11], so that it decays exponentially with the number of trees in a neighborhood of radius  $R$  around a given tree. Thus, for  $G$  we take the step function (limit  $p \rightarrow \infty$ )

$$G(|\mathbf{r}|) = \begin{cases} 1 & \text{if } |\mathbf{r}| \leq R \\ 0 & \text{if } |\mathbf{r}| > R, \end{cases} \quad (15)$$

where  $R$  is the interaction range that determines the competition distance among trees. For this kernel the Fourier transform is [27]  $\hat{G}(k) = 2\pi R^2 J_1(kR)/kR$  and its derivative is  $\hat{G}'(k) = -\pi R^2 J_2(kR)/k$ , where  $k \equiv |\mathbf{k}|$ , and  $J_i$  is the  $i^{\text{th}}$ -order Bessel function. Since  $\hat{G}(k)$  can take positive and negative values, pattern solutions may arise in the system, that will in turn depend on the values of  $\delta$  and  $\sigma$ . The most unstable mode is numerically obtained as  $k_c = 5.136/R$ . Because a pattern of  $n$  cells is characterized by a wavenumber  $k_c = 2\pi n/L$ , where  $L$  is the system size, the typical distance between clusters  $d_t = L/n$  is given by  $d_t \approx 1.22R$ , i.e., it is approximately the range of interaction  $R$ . This result is independent of the other parameters of the system.

The phase diagram of the model, computed numerically, is shown in Fig. 2, where depending on  $\delta$  and  $\sigma$  we plot the spatial character of the steady solution (homogeneous or inhomogeneous). Note that increasing competition enhances the inhomogeneous or pattern solution. This is because, as we are now in the case of a kernel giving rise to clusters, increasing  $\delta$  makes it more difficult to enter the exclusion zones in-between the clusters. For very strong competition (high, unrealistic,  $\delta$ ), fire has no influence on the pattern. However, for small to medium values of  $\delta$ , frequent fires (i.e., small  $\sigma$ ) enhances clustering since it also makes more difficult to enter into exclusion areas.

The critical line separating these two solutions (pattern and homogeneous) can be analytically computed as a function of the parameters  $\delta$ ,  $\sigma$ ,  $\rho_0$  and  $\hat{G}(k_c)$  (see Eq. (B.1) in Appendix B). In Figure 2 we have plotted (with crosses) this critical line separating homogeneous and pattern solutions for the step kernel. Note that the stationary density of trees,  $\rho_0$ , must be computed numerically from Eq. (7).

With  $b = 5$ , in the absence of fire ( $\sigma \rightarrow \infty$ ), and for weak competition, we can take the limits  $\delta \rightarrow 0$  and  $\sigma \rightarrow \infty$  of the dispersion relation Eq. (10), leading to

$$\lambda(k; \delta \rightarrow 0, \sigma \rightarrow \infty) = 4 - 10\rho_0, \quad (16)$$

which is negative for the typical density of trees in the system for these values of the parameters (See Fig. 1). This means that in this limit, trees are uniformly distributed in the system as there is no competition, and space does not play a relevant role in the establishment of new trees. This result agrees with the phase plane plotted in Figure 2. In biological terms, there are no exclusion zones in the system because there is no competition.

### 2.3. Numerical simulations

The previous analysis provides information, depending on the competition and fire parameters, about

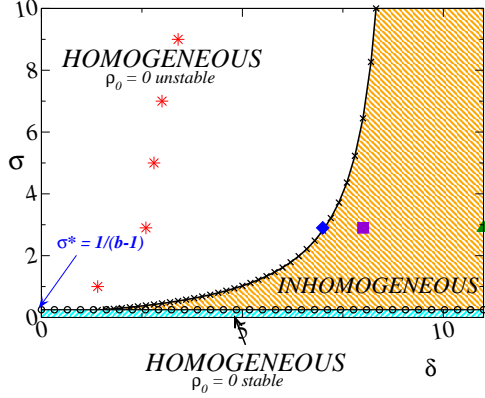


Figure 2: Possible solutions of the mean field equation Eq. (5) for  $b = 5.0$ ,  $\alpha = 1.0$ , and a step kernel. The absorbing-active transition in the mean field model is shown at  $\sigma^*$  with circles (o), as well as the homogeneous-pattern transition, indicated with crosses (x). The diamond, the square, and the up-triangle show the value of the parameters  $\sigma$  and  $\delta$  taken in Figures 3, 4, and 5 respectively. The stars point out the transition to inhomogeneous solutions in the stochastic model as described in Section 3, with  $\Gamma = 0.2$ .

when the solution is spatially homogenous and when trees arrange in clusters. However, the different shapes of the patterns have to be studied via numerical simulations [28] of the whole equation of the model. We have taken a finite square region of savanna with an area of 1 ha., allowed competition to occur in a circular area of radius  $R = 8$  m, and employed periodic boundary conditions and a finite differences algorithm to obtain the numerical solution. Similarly to what has been observed in previous studies [15, 17], different structures: gaps, stripes, and tree spots, are obtained in the stationary state as we make competition stronger given a fixed value of the fire frequency or, on the other hand, as we decrease the resistance to fires for a given competition intensity. In both equivalent cases, we observe this spectrum of patterns as far as we go to a more dry state of the system, where resources (mainly water) are more limited (see Figs. 3-5). It is notable that our modeling considers only nonlocal competition, and not, as already commented, short-range facilitation and long-range competition mechanisms as is typical in other studies [15, 17], which gives an idea of the robustness and relevance of these type of spatial patterns.

This same sequence of appearance of patterns has been already observed in [15] and indicates that, for a given value of the fire parameter, increasing  $\delta$ , i.e. decreasing the probability of surviving competition, new trees cannot establish into the exclusion areas so clustering is enhanced. Self-organized vegetation patterns can persist far into regions of high aridity where plants would become extinct if homogeneously distributed [15].

A much more quantitative analysis of the periodic-

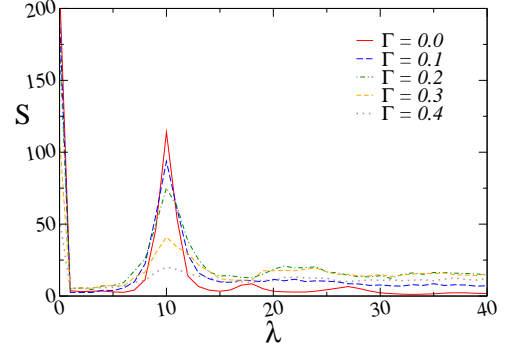


Figure 6: Structure function defined in equation (17) for different values of the demographic noise intensity. The main peak in  $\lambda = 10$  reveals the periodicity of the solution and the equivalence among patterns independent of the fluctuations.  $\delta = 9.8$ ,  $\sigma = 2.9$ ,  $R = 8$ ,  $\alpha = 1.0$ ,  $b = 5.0$ .

ity in the patterns can be performed via the structure function. This will be helpful to check the previous results and, especially, for the analysis of the data of the stochastic model of the next section, for which we will not present analytical results. The structure function is defined as the modulus of the spatial Fourier transform of the density of trees in the stationary state,

$$S(k) = \left\langle \left| \int d\mathbf{x} e^{i\mathbf{k}\cdot\mathbf{x}} \rho(\mathbf{x}, t \rightarrow \infty) \right| \right\rangle, \quad (17)$$

where the average is a spherical average over the wavevectors with modulus  $k$ . The structure function is helpful to study spatial periodicities in the system, similar to the power spectrum of a temporal signal. Its maximum identifies dominant periodicities, which in our case are the distances between tree clusters. Note that the geometry of the different patterns cannot be uncovered with the structure function, since this involves a spherical average. For our deterministic savanna model, the peak is always at  $\lambda_c = 10m$  (Figure 6 with  $\Gamma = 0$ ; this parameter will be defined later on), which is in good agreement with the theoretical result provided by the linear stability analysis  $\lambda = 2\pi/k_{max} = 9.78m$ .

### 3. Stochastic model

The perfectly periodic patterns emerging from the current deterministic model seem to be far from the disordered ones usually observed in aerial photographs and shown by individual based models [11]. Thus, to provide a reasonable description of the underlying small-scale birth and death dynamics, we add demographic noise to the standard deterministic equation, which will take into account the *intrinsic* fluctuations always present at the individual level.

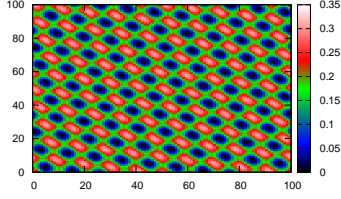


Figure 3: Grass spot pattern in the deterministic model pointed out with a diamond in Figure 2. The parameters are  $\delta = 7.0$ ,  $\sigma = 2.9$ ,  $R = 8.0$ ,  $b = 5.0$  and  $\alpha = 1.0$ .

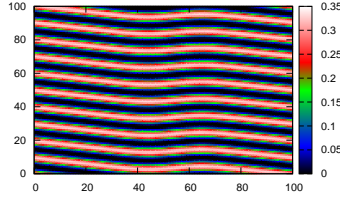


Figure 4: Striped pattern in the deterministic model pointed out with a square in Figure 2. The parameters are  $\delta = 8.0$ ,  $\sigma = 2.9$ ,  $R = 8.0$ ,  $b = 5.0$  and  $\alpha = 1.0$ .

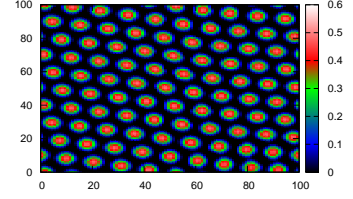


Figure 5: Tree spot pattern in the deterministic model pointed out with a triangle in Figure 2. The parameters are  $\delta = 11.0$ ,  $\sigma = 2.9$ ,  $R = 8.0$ ,  $b = 5.0$  and  $\alpha = 1.0$ .

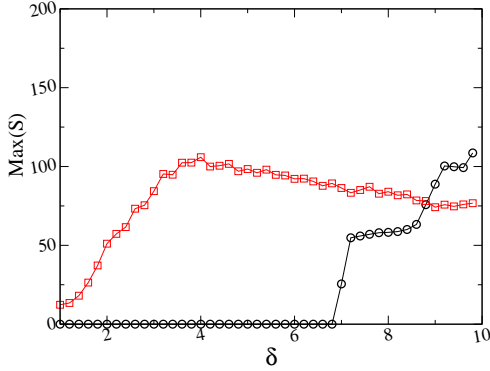


Figure 7: Maximum of the structure function for different values of the competition parameter  $\delta$  at long times. The fire parameter is fixed at  $\sigma = 2.9$ . Black circles show the transition to pattern in the deterministic model while red squares refer to the model with demographic noise,  $\Gamma = 0.20$ .

The interpretation of the field  $\rho(\mathbf{x}, t)$  is the density of tree (active) sites in a small volume,  $V$ . If we think of trees as reacting particles which are born and die probabilistically, the number of reactions taking place in a volume,  $V$ , is proportional to the number of particles therein,  $N$ , with small deviations. If  $N$  is large enough, the central limit theorem applies to the sum of  $N$  independent random variables and predicts that the amplitude of the deviation is of the order of  $\sqrt{N} \propto \sqrt{\rho(\mathbf{x}, t)}$  [29]. These fluctuations are referred to as demographic noise. The macroscopic equation is now stochastic,

$$\begin{aligned} \frac{\partial \rho(\mathbf{x}, t)}{\partial t} = & b_{eff}(\rho)[\rho(\mathbf{x}, t) - \rho^2(\mathbf{x}, t)] - \\ & - \alpha \rho(\mathbf{x}, t) + \Gamma \sqrt{\rho(\mathbf{x}, t)} \eta(\mathbf{x}, t), \end{aligned} \quad (18)$$

where  $\Gamma \propto \sqrt{b_{eff}}$  (but we take it as a constant, [30]) modulates the intensity of  $\eta(\mathbf{x}, t)$ , a Gaussian white noise term with zero mean and correlations

$$\langle \eta(\mathbf{x}, t) \eta(\mathbf{x}', t') \rangle = \delta(\mathbf{x} - \mathbf{x}') \delta(t - t'). \quad (19)$$

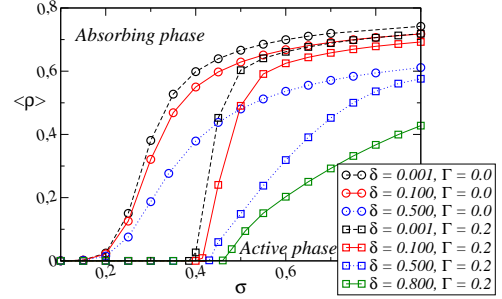


Figure 8: Active-absorbing phase transition both in the deterministic model (Circles) and considering the demographic noise (Squares). In the case of the stochastic model, we integrate the Eq. (18) with  $\Gamma = 0.2$  and average the density of trees in the steady state.

We first investigate the effect of intrinsic fluctuations on the persistence of trees in the system. We show (Fig. 8) that the critical point,  $\sigma^*$ , depends on the value of the competition parameter  $\delta$ . Increasing the competition strength, which implies a more arid savanna, makes trees less resistant fires. As is seen in the figure this effect is rather small, so that when  $\delta$  increases the transition to the grassland state appears only for a slightly larger  $\sigma$  (i.e., less frequent fire). The reason seems to be that fire frequency and intensity depend on grass biomass. Seasonally wet savannas support much more grass biomass that serves as a fuel for fires during dry season. Dry savannas have much lower grass biomass, so they don't burn as often or as intensely.

We numerically explore the stochastic savanna model using an algorithm developed in [30]. Note that the noise makes the transition smoother so the change from homogeneous to inhomogeneous spatial patterns is not as clear as it is in the limit where the demographic noise vanishes (See Fig. 7). Figure 7 also shows how the maximum of the structure function decays with the competition strength when demographic

fluctuations are considered. As we are keeping the resistance to fires fixed, increasing the competition intensity takes the system towards the absorbing phase, where the solution is homogeneous and the structure function shows no peaks.

We have studied the dynamics of the system for some values of the fire and competition parameters, focusing on the role of the noise strength  $\Gamma$ . Despite the obvious increasing randomness in the patterns with  $\Gamma$  (Figures 9,10), they are statistically equivalent to those in the deterministic model (See the structure function in Figure 6, peaked around  $\lambda = 10$ ). Therefore, the model presents an active-absorbing transition with the noise strength,  $\Gamma$ , being the control parameter, and we obtain (more realistic) irregular patterns of trees in the whole clustered region, where the shape of the pattern in the deterministic model is not relevant. We also find (shown with stars in Fig. 2) that the appearance of patterns in the system now occurs at lower values of the competition parameter,  $\delta$ , than in the no noise limit, but the shape of the transition line remains qualitatively similar.

#### 4. Discussion

The striking observed spatial arrangements of savanna trees have led to speculation on the mechanisms producing these patterns [5–7, 9, 10, 15]. A key step in such an analysis is defining the most parsimonious combination of mechanisms that will produce the pattern in question. The literature on savanna tree spatial patterning with kernel-based models has tended to focus on the interplay between local facilitation and long-range competition, under the assumption that both are essential for pattern formation [13–16]. Following Rietkerk and van de Koppel’s [8] observation that not all of the ecosystems in their review of spatial patterning featured a clear short-range facilitation mechanism, we have studied the conditions under which long-range competition alone could account for savanna tree spatial pattern.

We have shown that nonlocal competition, acting without facilitation, is indeed sufficient to induce the full range of observed spatial patterns, provided the competition term enters nonlinearly in the equation for the density of trees, and that competition is strong enough, so resources in the system are limited. The key technical requirement for this effect to occur is that the Fourier transform of the competition kernel becomes negative for certain values of the wavenumber,  $k$ . In practice this means that kernels whose Fourier transform takes negative values for some wavenumber values, will lead to competition driven clustering. The

other mechanism we have considered for a minimalistic but realistic savanna model, fire, has been shown to be relevant for the coexistence of trees and grass and for the shape of the patterns. However, competition is the main ingredient allowing pattern solutions to exist in the model. If the shape of the kernel allows these types of solutions, then the specific values of fire and competition parameters determine the kind of spatial structure that develops. It is also worth to mention that one can observe the full spectrum of patterns in the limit where fires vanish ( $\sigma \rightarrow \infty$ ) as we increase the competition, but not when there is not competition,  $\delta = 0$ , regardless of the value of the fire term. Therefore, we conclude that the nonlocal competition term is the responsible of the emergence of clustered distributions of trees in the model, with the fire term playing a relevant role when it comes to fixing the value of the competition parameter at which patterns appear.

These findings have the potential to shift the focus of the debate over the role of short-range factors on large-scale savanna tree spatial pattern. Our results demonstrate that short-range facilitation is not a necessary condition for pattern formation, suggesting that the precise balance of positive and negative short-range forces may have little or no effect on large-scale pattern in real savannas. While understanding the net effects of these short-range interactions among trees may be relevant for other aspects of savanna tree ecology, our results suggest that, when spatial pattern is the focus, emphasis should instead shift to identifying when, where, and to what extent nonlocal competition will be important.

The other important feature of savannas, the characteristic long-time coexistence of trees and grass is well captured with our model (Figures 1 and 8). Besides, introducing demographic fluctuations, as it is shown in Figure 8, makes our approach much more realistic, since the persistence of trees in the face of fires is related to the water in the system. On the other hand, demographic stochasticity causes tree extinction at lower fire frequencies than in the deterministic case, because random fluctuations in tree density are of sufficient magnitude that tree density can hit zero even if the deterministic stationary tree density (for a given fire frequency) is greater than zero.

#### 5. Summary

We have shown the formation of patterns in a minimal spatially nonlocal savanna model, as well as the transition from a state where trees and grass coexist to an absorbing one, where only grass is present. The salient feature of the model is that it only considers nonlocal (and nonlinear) competition, which differs



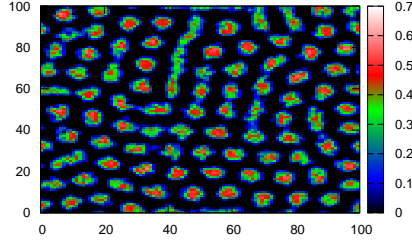


Figure 9: Irregular pattern in the model with demographic noise. The parameters are  $\Gamma = 0.10$ ,  $\delta = 11.0$ ,  $\sigma = 2.9$ ,  $R = 8.0$ ,  $b = 5.0$  and  $\alpha = 1.0$ .

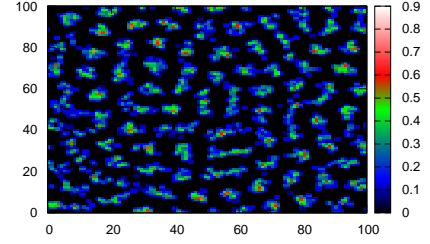


Figure 10: Irregular pattern in the model with demographic noise. The parameters are  $\Gamma = 0.20$ ,  $\delta = 11.0$ ,  $\sigma = 2.9$ ,  $R = 8.0$ ,  $b = 5.0$  and  $\alpha = 1.0$ .

from standard kernel-based savanna models that feature both short-range facilitation and long-range competition. The same sequence of spatial patterns appears in both approaches, confirming Rietkerk and van de Koppel's [8] suggestion that short-range facilitation may not be a necessary condition for spatial pattern formation.

Inspired by [11], we have proposed a nonlocal deterministic macroscopic equation for the evolution of the local density of trees where fire and tree-tree competition are the dominant mechanisms. It is a nonlocal interaction model like the kernel-based models [2] for vegetation pattern formation in arid ecosystems, but while the kernel function is usually used to account for the short-range facilitation and long-range competition, we use it exclusively to define the competition neighborhood (the length scale of the interaction). In other words, our approach only considers competitive interactions, without facilitation. If the kernel function falls off with distance very quickly (the Fourier transform is always positive) the system only has homogenous solutions. In the opposite case, patterns may appear depending on system parameters (fire and interaction strength), and in a sequence similar to the spatial structures appearing in standard kernel-based models. Under less favorable environmental conditions, trees tend to arrange in more robust structures to survive (Fig. 5). Biologically, trees are lumped in dense groups, separated by empty regions. Entrance of new trees in these *exclusion zones* is impossible due to the intense competition they experience there.

This deterministic treatment is formal, and we have shown the different spatial distributions of the trees that occur as competition becomes more intense, concluding that self organization of trees is a good mechanism to promote tree survival in extremely arid conditions [15]. Trees tend to cluster in the high competition (few resources) limit (Fig. 5), due to the formation of exclusion zones caused by non-local competition,

and *not* as a result of local facilitation. However, because we are dealing with a deterministic model, the patterns are too regular and the transition between the grass-only and a tree-populated states is independent of tree competition. Fluctuations, due to the stochastic nature of individual birth and death events, are included for a more realistic description. Calabrese et al. [11] also noted that savanna-to-grassland transition was independent of competition intensity in the deterministic case, but not in the stochastic case. In the present model, both the grassland to savanna transition and the spatial structures that develop are influenced by demographic stochasticity.

We have quantified the characteristic spacing of spatial patterns through the structure function. The irregular patterns produced by the stochastic model still have a dominant wavelength whose value is the same as in the deterministic model and depends only on the value of the range of the interaction,  $R$  in the kernel function. The match between the typical spatial scale of the patterns and the characteristic distance over which nonlocal competition acts indicates that competition is responsible for the presence of clustered spatial structures.

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## Appendix A. Linear stability analysis

This appendix shows the details of the linear stability analysis, in particular how the dispersion relation in Eq. (10) is obtained. We consider the stationary solution  $\rho_0$  plus a small perturbation,

$$\rho(\mathbf{x}, t) = \rho_0 + \epsilon \psi(\mathbf{x}, t), \quad (\text{A.1})$$



where  $\epsilon \ll 1$ . Substituting Eq. (A.1) into the original equation (5) and retaining only linear terms in  $\epsilon$ , and then taking harmonic perturbations of the type  $\psi(\mathbf{x}, t) = \exp(\lambda t - i\mathbf{k} \cdot \mathbf{x})$ , we arrive to the relation dispersion

$$\lambda(k) = bC\sigma(\rho_0 - \rho_0^2) \left[ \frac{1}{(\sigma+1-\rho_0)^2} - \frac{\hat{G}(k)\delta}{\sigma+1-\rho_0} \right] + bC\sigma \frac{1-2\rho_0}{\sigma+1-\rho_0} - \alpha, \quad (\text{A.2})$$

where  $\hat{G}$  is the Fourier transform of the kernel and  $C \equiv \exp \left[ -\delta \rho_0 \int G(\mathbf{x} - \mathbf{x}') d\mathbf{x}' \right]$ . This expression can be written as Eq. (10) using the definition of  $b_{eff}(\rho_0)$  and taking  $\alpha = 1$ .

## Appendix B. Expression of the transition to pattern critical line.

We show here the analytical expression for the critical line in the transition from homogeneous to inhomogeneous solutions. Starting from Eq. (12) it is possible to write an expression for the value of the resistance to fires parameter,  $\sigma$ , at which the macroscopic equation (5) starts showing pattern solutions, as a function of the competition parameter,  $\delta$ , and the most unstable mode  $k_c$ . Considering the value of the parameters taken in our study,  $b = 5$  and  $\alpha = 1$ , it is

$$\sigma_c = \frac{(\rho_0-1)[5(\rho_0-1)(\delta\hat{G}(k_c)\rho_0-1)-2e^{\delta\pi R^2\rho_0}]}{10[1-2\rho_0+\delta\hat{G}(k_c)\rho_0(1+\rho_0)-e^{\delta\pi R^2\rho_0}/5]} + \frac{(\rho_0-1)\sqrt{5[5(\rho_0-1)^2(\delta\hat{G}(k_c)\rho_0-1)^2-4e^{\delta\pi R^2\rho_0}\rho_0]}}{10[1-2\rho_0+\delta\hat{G}(k_c)\rho_0(1+\rho_0)-e^{\delta\pi R^2\rho_0}/5]}. \quad (\text{B.1})$$

This complicated expression must be evaluated numerically together with the solution of Eq. (7) for the stationary density of trees, which is also a function of the competition and fire parameters. We show the results in Figure 2, where the curve, represented with the black crosses, fits perfectly with the numerical results from the linear stability analysis.

## Appendix C. The effect of rainfall: Random switching between death and birth

One of the key ingredients for the long coexistence between grass and trees is the largely inhomogeneous temporal distribution of precipitations over time [3, 28]. We have studied this environmental variability following the idea in [18], considering the switching between unstressed vegetation growth, given by the first term in (5), and drought-induced vegetation decay, represented with the second term in Eq. (5). These

processes take place each time step with probability  $P$  and  $1 - P$ , respectively. From now on, we call

$$\begin{aligned} f_b[\rho(\mathbf{x}, t)] &= b_{eff}(\rho) [\rho(\mathbf{x}, t) - \rho^2(\mathbf{x}, t)], \\ f_d[\rho(\mathbf{x}, t)] &= -\alpha\rho(\mathbf{x}, t), \end{aligned} \quad (\text{C.1})$$

and

$$f_{\pm}[\rho(\mathbf{x}, t)] = \frac{1}{2} [f_b[\rho(\mathbf{x}, t)] \pm f_d[\rho(\mathbf{x}, t)]]. \quad (\text{C.2})$$

The random dynamics of the system is written in terms of a stochastic partial differential equation,

$$\frac{\partial \rho(\mathbf{x}, t)}{\partial t} = f_+[\rho(\mathbf{x}, t)] + f_-[\rho(\mathbf{x}, t)]\xi_{dn}(t), \quad (\text{C.3})$$

where  $\xi_{dn}(t)$  is a dichotomous noise (DMN), assuming values  $+1$  (wet season) and  $-1$  (dry season) with probability  $P$  and  $1 - P$ , respectively.

If the rate of random switching, here taken as the inverse of the integration time step, is relatively fast respect to the rate of convergence to equilibrium in each of the two states, we can replace the noise term in Eq. (C.3) with its average value,  $\langle \xi_{dn}(t) \rangle = 1 - 2P$ . It is meaningful since the rainfall seasons are much shorter than the time needed to reach one of the equilibrium stationary states of death and birth processes,  $\rho(\mathbf{x}, t) = 0, 1$ , respectively. This substitution leads to a deterministic equation

$$\frac{\partial \rho(\mathbf{x}, t)}{\partial t} = f_+[\rho(\mathbf{x}, t)] + f_-[\rho(\mathbf{x}, t)](1 - 2P), \quad (\text{C.4})$$

where we will be able to perform linear stability analysis as usual. The new dispersion relation is easily obtained,

$$\begin{aligned} \lambda(k; \sigma, \delta) &= b_{eff}(\rho_0)P \frac{1+\sigma(1-2\rho_0)}{\sigma-\rho_0+1} - (1 - P) \\ &\quad - b_{eff}(\rho_0)P \frac{\rho_0[2-\rho_0+\delta\hat{G}(k)(\rho_0-1)(\rho_0-1-\sigma)+2\sigma]}{(\sigma-\rho_0+1)}, \end{aligned} \quad (\text{C.5})$$

which means that the main effect of the dichotomous noise is to renormalize the rates  $\alpha$  and  $b$ . The patterns observed now are the same as the ones in the deterministic case, though the regions where they emerge change in accordance with this renormalization. Thus, the effect of stochastic precipitation, as modeled with this random switching mechanism, is a change of the parameter values for the different transitions observed in the deterministic continuum model Eq. (5).

According to the value of  $P$ , an absorbing-active phase transition is observed,  $P_c \approx 0.20$ . Small values of  $P$ , meaning long dry season, lead to an absorbing state while increasing the probability of raining implies the appearance of trees in the system. In this latter case, the solution can be either homogeneous or showing spatial patterns, depending on fire and competition.

This attempt to model rainfall has not been very successful and does not give a lot of new information. Much effort of future research should be put on this point, trying to get much more realistic modelling of external environmental variability, according to empirical observations, with long runs of dry years and rare wet years.

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